THE EXISTENCE OF A SHORT REPRODUCTIVE CYCLE IN *ANODONTA IMBECILLIS*.

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Fresh water mussels of North America have been classed by Sterki (1895) as summer or winter breeders. He notes that in winter breeders fertilization of ova occurs in the late summer, embryonic development is completed and the fully developed glochidia are carried through the winter in the maternal marsupia and discharged in the following spring. In the summer breeders fertilization occurs in the late spring or early summer and the fully formed glochidia are discharged "as a rule by the end of August."

Lefevre and Curtis (1912) prefer to designate these two classes as long and short term breeders. They include *Anodonta* in the former group, and although *A. imbecillis* is not listed in the data from which their conclusions are drawn, the statement is made that the breeding season is a generic character, "all species of a genus having essentially the same period of gravidity."

In a table compiled by Coker, Shira, Clark, and Howard (1919) gravid *Anodonta imbecillis* are listed for all months with the exception of April.

Anodonta imbecillis, although not important commercially, is of interest for two reasons; first, it is one of the two known species which carry the young in the marsupia during metamorphosis from glochidia to juvenile mussels, thus eliminating the parasitic stage on fishes which other species undergo, and, second, it is one of the few species which are hermaphroditic (Sterki, 1898).

During the summer of 1922 the writer attempted to work out a method of aparasitic mussel culture of commercially valuable mussels. One line of attacking this problem which seemed to offer promise of results was to simulate conditions pertaining in metamorphosis during the intra-marsupial life of aparasitic forms. Therefore a series of observations was begun on *Anodonta imbecillis* during the course of which successive examinations

were made at intervals of several days on more than one hundred individuals. This has furnished the following evidence for a shorter reproductive cycle than formerly reported for this species.

Material and Method.

Anodonta imbecillis is commonly called the "paper shell" because of the extreme thinness of the valves. Possibly correlated with this economy in shell formation, is its rapid rate of growth. It may begin to reproduce during the second year. The observations in this paper were made on two- and three-year-old mussels.

In this species the outer gills serve as marsupia. It is an easy matter to insert a capillary pipette between the valves, make a single puncture in the marsupium, and remove some of its contents with only slight injury to the mussel. This puncture heals rapidly. In order that the least possible modification of reproductive activity might be produced by this examination, the samples removed were small, containing only from 20 to 40 individuals. The puncture was made in a direction parallel to the long axis of the gill so that the sample removed contained young from several gill compartments.

Relatively slight disturbances may cause "abortion" of marsupial contents in some species. Lefevre and Curtis, however, note that they have never observed abortion in *Anodonta*. The thin shell of *A. imbecillis* renders the above described operation very simple as the valves may be opened for the insertion of the pipette with the thumb nails. This probably eliminates the possibility of abortion as a factor bearing upon the following evidence.

The examinations extended over a period of one and one half months from the middle of July to early in September.

Most of the mussels studied were taken from the main supply reservoir of the U. S. Fisheries Biological Station at Fairport, Iowa, which is supplied daily from the Mississippi River. A few preliminary observations were made on mussels taken from the river.

Throughout the observations they were kept in running water in experimental troughs supplied from a pond containing an abundance of pond life. As opportunity for considerable sedi-

mentation was afforded, this supply was much clearer than water from the river or reservoir. The fact that very successful yields were obtained in artificial mussel culture experiments carried on simultaneously under these conditions by Dr. A. D. Howard and B. J. Anson excludes any possible intervention of adverse environmental conditions.

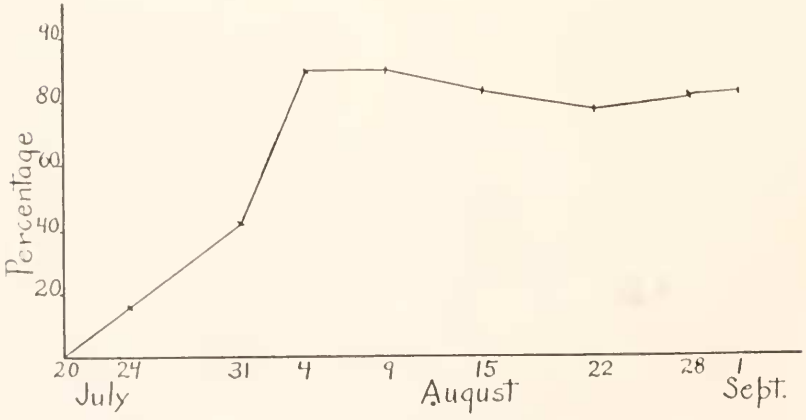
Observations.

Between July 15 and 20 about two dozen mussels were examined without finding a gravid individual. On July 24, 5 of 33 examined (15 per cent.) contained early embryonic stages. Nineteen of these 33 were observed repeatedly until September 1. On July 31, 8, including the five already noted (42 per cent.), contained embryos. On August 4, 17 or 89.5 per cent. were gravid. Larger numbers of this species were examined during August. From August 8 to September 1 the percentage of mussels bearing embryos, glochidia, or young in various stages of metamorphosis never dropped below 77.2 per cent. (see Table I. and Graph 1).

TABLE I.

Percentage of Mussels Bearing Embryos or Glochidia.

Date	7/15–20	7/24	8/4	8/9	8/15	8/22	8/28	9/1
Number examined	20–24	33	19	69	101	105	103	57
Percentage	0	15.1	89.5	89.9	83.2	77.2	80.6	82.5



Graph 1. Percentage of mussels bearing embryos or glochidia.

The conclusion drawn is that the reproductive season of *Anodonta imbecillis* in this location begins during the latter part of July.

As these observations were continued the various stages of embryonic development and glochidial metamorphosis were identified and data accumulated as to the time required for this transition. Eleven different stages were identified as follows:[1]

1. Early segmentation of the fertilized ovum.

2. Later segmentation.

3. Early differentiation of the single anlage of the valves which at this stage caps the segmenting cell mass.

4. Formation of a groove in this "cap" which divides it into two separate valve anlagen.

5. The developing valves lie on the segmenting cell mass "like continents in relief on the globe."

6. The two valves resemble a folded leaf which now completely encloses the future "soft parts" of the young larva.

7. The glochidial shape is attained but the larva is still colorless and transparent. The single glochidial adductor muscle can be seen to quiver or "flash" although the valves are closed.

8. The glochidia are now fully formed, have a rich yellow color, and a single adductor muscle. Many may be seen to snap vigorously if freed from the egg membranes in the process of removal from the marsupia. Those within the membranes have their valves opened. This stage is equivalent to that at which the glochidia of species dependent on parasitism on fishes for metamorphosis are extruded from the marsupia.

9. Mid-metamorphosis; rich yellow in color, no adductor muscle visible.

10. Late metamorphosis; the two definitive adductor muscles are now visible. Snapping of the valves cannot be induced by freeing the glochidia from their egg membranes.

11. Juvenile mussels; the foot is now visible, active snapping of the valves and extension of the foot occurs.

[1] No attempt was made to describe fully the various stages of development; they are merely characterized for greater accuracy in determining the duration of developmental stages. Examination was made with a binocular microscope magnifying × 50.

Even juvenile mussels are found within the egg membranes. A stringy transparent gel forms or is secreted about the egg membrane enclosing the developing embryos after they reach the marsupia. It is well formed by the stage at which they begin to turn yellow and partly disappears in late metamorphosis.

Table II. includes observations on twenty typical individuals. More than one hundred are included in the data from which the average time required for the transition between stages is determined.

TABLE II.

STAGES OF DEVELOPMENT OF YOUNG IN MARSUPIA OF *A. imbecillis*.[2]

No. of Mussel.	Date.								
	7/24	7/27	7/31	8/4	8/9	8/15	8/22	8/28	9/1
1	3	4	6	7	8	9	0	0	1
2	3	4	6	7	8	9	0	3	4
3	3	4	5	6–7	8	9	0	1	1–2
4	6	7	8	9	0	0	0	0	1
5	:	:	3	4	6	:	9	0	1
6	:	:	3	4	6	8	9	0	0
7	:	:	7	8	9	0	0	1	3
8	:	:	:	8	9	1	3	7–8	9
9	:	:	:	8–9	0	0	1	4	7
10	:	:	:	5	7	8–9	0	0	3
11	:	:	:	6	7	8–9	0	1	3
12	:	:	:	5	7	8–9	0	0	3
13	:	:	:	1–2	5	7	8–9	0	3
14	:	:	:	1	5	7	9	1	4
15	:	:	:	3	4	6	8–9	0	3
16	:	:	:	4	6–7	7–8	9	0	1
17	:	:	:	1	4	6	9	10–11	0
18	:	:	:	0	0	1	5	8	9
19	:	:	:	0	1	5	7–8	10–11	0
20	:	:	:	6	8	10	0	1	3

Numbers 13, 14, 17, 19 underwent a complete reproductive cycle in from 22 to 27 days during August. The calculation of cycle duration by averaging parts of cycles from all available data gives an average cycle duration of 3 to 4 weeks. This period then provides time for fertilization, segmentation, embryonic development to the glochidial or larval stage, and metamorphosis of the glochidium into the juvenile mussel. In *Anodonta imbecillis* it all occurs in the maternal marsupium, with the possible exception of fertilization. Metamorphosis, which in

[2] 0 in the table indicates empty marsupia during the interval between reproductive cycles. Numbers refer to stages characterized in the text.

other forms occurs in epithelial "cysts" on the gills of fishes, requires in this species only 7–10 days, as compared with a minimum of 12–14 in *Lampsilis anodontoides* and *L. luteola*. Development from the fertilized ovum to the fully formed glochidium may occur in two weeks' time.

The duration of the interval between reproductive cycles varies from 2 or 3 days to 2 (or rarely 3)weeks.

It is realized that more extensive observations would provide material for more accurate determination of the duration of various stages of this cycle and the possible changes in these time relations during the fall and winter months.

However, the data at hand does warrant the conclusion that *Anodonta imbecillis* cannot properly be classed as a long term breeder. Juveniles are discharged during the latter half of August and first half of September and a new reproductive cycle begins. Whether this cycle is repeated throughout the months when this species is listed as gravid is still to be determined.

Discussion.

The possible correlation of the rapid rate of growth and the early attainment of sexual maturity of *Anodonta imbecillis* with the thin "paper shell" has already been mentioned. It is possible that this short reproductive cycle may be correlated with these factors.

No attempt was made to determine whether self or cross fertilization is the normal process in *Anodonta imbecillis*. If self fertilization is the rule, hermaphroditism may have been a contributing factor in the establishment of a shorter reproductive cycle.

Since to date only two species have been reported as developing aparasitically, the idea that they may have depended at one time upon parasitic metamorphosis, but later evolved an ability to develop independently, seems natural. Many investigators have commented on the existence of small hooks at the valve edges as constituting the remains of a former parasitic adaptation. Since parasitism on fishes which make seasonal upstream migrations furnishes an efficient method of distribution (possibly the only method of extensive upstream migration of mussels), a wide distribution of aparasitic forms would lend added weight to

this theory. But if the natural course of evolution of reproduction be followed, parasitism must be considered a secondary development. It is possible therefore that metamorphosis without parasitism is the primitive method and that *Anodonta imbecillis* never has relied upon parasitism for development. It is also possible that the shorter reproductive cycle is the primitive one rather than an adaptation from one similar to that of other species of Unionidae.

Summary.

Anodonta imbecillis cannot be classed with either long or short term breeders as defined by Lefevre and Curtis. In specimens obtained at Fairport, Iowa, a complete reproductive cycle (including metamorphosis from glochidia to juvenile mussels, for reproduction in this species does not depend on parasitism) is completed in from 3 to 4 weeks during the late summer. Another cycle begins after an interval varying from 2 to 3 days to 2 weeks. Gravid *A. imbecillis* have been found in all months but April. It is possible therefore that this short reproductive cycle is repeated throughout the year.

Literature Cited.

Coker, R. E., Shira, A. F., Clark, H. W., Howard, A. D.

'19-'20 Natural History and Propagation of Fresh Water Mussels. Bul. Bureau Fisheries, Vol. 37, No. 893.

Howard, A. D.

'15 Some Exceptional Cases of Breeding among the Unionidea. Nautilus, Vol. 29, p. 4–11.

Howard, A. D., and Anson, B. J.

'22 Phases in the Parasitism of the Unionidæ. Jour. Parasitology, Vol. 22, p. 68.

Lefevre, G. and Curtis, W. C.

'12 Studies on the Reproduction and Artificial Propagation of Fresh Water Mussels. Bul. Bureau Fisheries, Vol. 30.

Lillie, F. R.

'95 The Embryology of the Unionidæ. Jour. Morph., Vol. 10, p. 1–100.